AMERICAN MUSEUM NOVITATES

Number 3825, 24 pp. February 24, 2015

New genera and species of Plokiophilidae from Australia, Fiji, and Southeast Asia, with a revised classification of the family (Insecta: Heteroptera: Cimicoidea)

RANDALL SCHUH,[1] PAVEL ŠTYS,[2] GERASIMOS CASSIS,[3] MARGARET LEHNERT,[4] DUSTIN SWANSON,[5] AND TERRI BRUCE[6]

ABSTRACT

Monteithophila queenslandana, new genus and new species, is described from Queensland, Australia, and represents the first record of the family Plokiophilidae from the continent. Morphology of the male genitalia is similar to that found in *Heissophila* Schuh from Thailand and therefore the traumatic insemination as found in other members of the family is hypothesized to be absent in *Monteithophila*. The female of an apparently congeneric taxon from Fiji is described as *Monteithophila fijiensis*. *Paraplokiophiloides schwendingeri*, new genus and new species, is described from Thailand. Female genitalic morphology in the Plokiophilidae is documented with laser confocal microscopy. A revised classification of the Plokiophilidae is proposed in order to establish congruence between observed morphological characters and the recognized higher-taxonomic groupings. The new subfamily Heissophilinae is erected to include *Heissophila*, *Moneithophila*, and the Baltic amber fossil *Pavlostysia* Popov. The concept

[1] Division of Invertebrate Zoology American Museum of Natural History.
[2] Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic.
[3] School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia.
[4] Department of Biological Sciences, Kent State University at Stark, North Canton, Ohio.
[5] Thomas More College, Crestview Hills, Kentucky.
[6] Clemson Light Imaging Facility, College of Agriculture, Forestry, and Life Sciences, Clemson University, Clemson, South Carolina.

Copyright © American Museum of Natural History 2015 ISSN 0003-0082

of Plokiophilinae is revised to include all taxa with traumatic insemination. The tribe Lipokophilini is erected to contain the Recent genus *Lipokophila* Štys. A newly delimited Plokiophilini includes the subtribes Embiophilina and Plokiophilina; *Paraplokiophiloides* is placed in the Embiophilina based on the presence of fore- and mesofemoral spines. Defining characters of the Plokiophilidae are discussed and a key to the genera is included.

INTRODUCTION

Members of the Plokiophilidae are known for their almost exclusive occurrence in the webs of spiders of the suborders Mygalomorphae (China and Myers, 1929; Schuh, 2006) and Araneomorphae (Carayon, 1974; Eberhard et al., 1993) as well as of the insect order Embiidina. Phylogenetic analyses of relationships within the Cimicomorpha indicate that Plokiophilidae are members of the Cimicoidea (Ford, 1976; Schuh and Štys, 1991; Schuh et al., 2009; Jung et al., 2010; Jung and Lee, 2012), although their family placement was long in dispute (China and Myers, 1929; China, 1953; Carayon, 1961, 1974). Carayon (1974) provided a detailed classification of the Plokiophilidae with the recognition of two subfamilies, Embiophilinae and Plokiophilinae: the former possessed heavy forefemoral spines and lived in the webs of Embiidina, the latter lacked forefemoral spines and lived in the webs of spiders. Carayon (1961, 1974) showed on the basis of morphological, histological, and direct observations that copulation in *Plokiophila* China, *Plokiophiloides* Carayon, *Lipokophila* Štys, and *Embiophila* (*Acaldina*) Carayon takes place via traumatic insemination. The presumption was that all members of the group practiced traumatic insemination and that this attribute was either a defining feature of the group or was a synapomorphy of Plokiophilidae and the remaining Cimicoidea (Ford, 1976; Schuh, 1986; Schuh and Stys, 1991). Furthermore, members of the group were known to occur only in the New World tropics, including Cuba, and tropical Africa. Schuh (2006), in his description of *Heissophila* from Thailand, expanded the known distribution of the group to include the Asian tropics and concluded, based on male genitalic structure, that traumatic insemination via copulatory tubes or puncture of the abdominal wall is absent in that group. Schuh (2006) went on to suggest that a new classification for the group might be required to accommodate the strikingly different male genitalic morphology seen in *Heissophila* as compared to all other known Plokiophilidae.

In the present paper we provide additional documentation for the Plokiophilidae, including the description of new taxa, additional documentation of morphology, and expansion of the known distribution for the group. These observations, in conjunction with existing information, are used to argue for a revised classification of the group.

First, we describe *Monteithophila*, new genus, with two new species, this taxon representing the first record of Plokiophilidae in both Australia and Fiji. *Monteithophila* is shown through the use of light and scanning electron microscopy to have male and female genitalic morphology similar to that of *Heissophila*. On the basis of morphology we postulate that *Monteithophila* and *Heissophila* lack the specialized mechanisms of traumatic insemination found in all other members of the Plokiophilidae. Second, we describe the new genus and new species *Paraplokiophiloides schwendingeri* from Thailand, this taxon representing the first record of Plokiophili-

dae with traumatic insemination in tropical Asia, and one that has a combination of characters not seen in any previously described taxon. Third, we demonstrate through the use of laser confocal microscopy that the females of *Heissophila* lack copulatory tubes, thereby corroborating the assertion of Schuh (2006), based on male genitalic structure, that traumatic insemination via copulatory tubes or puncture of the abdominal wall is absent in that group. Finally, we provide the first records for *Heissophila macrotheleae* Schuh from East Kalimantan (Borneo) and additional records from Thailand.

In order to accommodate the novel male genitalic morphology seen in *Heissophila* and *Monteithophila*, the character complement of *Paraplokiophiloides*, as well as those of *Lipokophila* Štys from the New World and *Pavlostysia* Popov from Baltic amber, and their impact on the existing classification of the Plokiophilinae, we offer a revised classification of the family. In order to facilitate the use of that classification we provide a key to the higher taxa and genera of Plokiophilidae.

MATERIALS AND METHODS

Scanning Electron Microscopy: Micrographs were prepared using a Hitachi 4300 instrument at the American Museum of Natural History (AMNH). Specimens were coated with gold-palladium before observation.

Photomicrographic methods: Habitus images of *Monteithophila queenslandana* we captured using a Visionary Digital imaging system produced by Roy Larimer with a Canon DSLR, Infinity Long-Distance Microscope, and stacking software. Images of *Monteithophila fijiensis* and *Paraplokiophiloides schwendingeri* were captured using a Leica MZ16A with a Leica digital camera and stacking software.

Confocal microscopy methods: Abdomens of specimens were mounted on microscope slides according to the methods of Borkent and Spinelli (2007). Briefly, abdomens were placed in 10% KOH in a double boiler for three minutes, transferred to 15% acetic acid for 15 min, 2-propanol for 15 min, 2-propanol over 100% clove oil for 20–60 min (until specimen sunk into clove oil layer), and 100% clove oil for 30 min, and finally mounted in Canada balsam thinned with clove oil. Images of specimen autofluorescence were taken using a Nikon Ti Eclipse microscope equipped with a C1si laser spectral confocal scanhead (objective: 10×, Plan Apo; NA= 0.45; standard TRITC settings Ex/Em [561/578 nm]).

Measurements: All measurements are in mm. We present information only for the holotypes and for an individual of the opposite sex, where available.

Specimen deposition: Specimen materials used in the present study are housed in the following institutions; curators or others responsible for loan of material are listed after the institution:

AMNH, American Museum of Natural History, New York, Randall T. Schuh

MNVG, Museum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland, Peter Schwendinger

QM, Queensland Museum, Brisbane, Geoff Monteith

The descriptions in the present paper are patterned after the description of *Heissophila* Schuh to assist in making comparisons of taxa.

TAXONOMY AND MORPHOLOGY

Monteithophila Schuh, Štys, and Cassis, new genus

Type Species: *Monteithophila queenslandana* Schuh, Štys, and Cassis, new species, by present designation.

Diagnosis: Among all Plokiophilidae most similar to *Heissophila* in the possession of a conventional broadly attached pygophore with symmetrical parameres lying exposed on the dorsal surface (fig. 5G), although the apices of the parameres directed anteromedially in *Monteithophila* rather than posterolaterally as in *Heissophila*; tarsi 3-segmented, an attribute also occurring in *Heissophila,* the New World plokiophiline genus *Lipokophila* Štys, and the Baltic amber fossil taxon *Pavlostsyia* Popov. Fossula spongiosa lacking on all legs. Costal fracture absent, corial glands numerous, occurring on nearly entire clavus and corium.

Description: *Male*: Small, elongate; total length 2.41, width pronotum 0.67. SURFACE AND VESTITURE (figs.1, 3): Vestiture of dorsum and venter comprising short, reclining, simple setae (figs. 1A–D, 3A), setae on head and pronotum sometimes longer and more nearly erect (fig. 6). Antennae and tibiae with short reclining setae, length equal to or less than diameter of antennal segment 2 (pedicel). Macrochetae (Carayon, 1974; sometimes referred to as cephalic trichobothria, e.g., Schuh and Slater, 1995) on head indistinguishable from common setae (fig. 4A); eye with two setae inserted near posterior margin (figs. 2E, 4A, B); pronotum without an elongate seta (macrocheta) on anterolateral angle as recorded by Carayon (1974) for other Plokiophilidae (see fig. 7A, B for *Paraplokiophiloides schwendingeri*); abdominal segment 8 without an obviously elongate macrocheta laterally as seen in *Heissophila* (Schuh, 2006: fig. 4A). STRUCTURE: **Head** (figs. 2B, D–G, 4A, B): Roughly cylindrical, weakly elongate anteroposteriorly, projecting beyond anterior margin of eye by about the length of eye; vertex and frons sloping at same angle as weakly prominent clypeus (figs. 2D, 4B); buccal cavity more or less round, directed anteroventrally, removed from posterior margin of head by gula of length somewhat greater than longitudinal diameter of eye in lateral view (figs. 2D, 4A, B); mandibular and maxillary plates small (fig. 4B); buccula relatively broad but not distinctly demarcated from head (figs. 2D, 4A, B). Labium elongate, slender, tapering to acute apex, reaching to anterior margin of hind coxa, segment 1 short and broad (fig. 2D, 4A, B), ratio of length of segments 1:3:4:7. Eyes relatively small in dorsal view, removed from anterior margin of pronotum by about the diameter of antennal segment 2 (figs. 1A–D, 4A); eyes in lateral view occupying one-half to two-thirds height of head, elongate oval and narrowing ventrally, posterior margin nearly straight (figs. 2D, 4B, 6); antennal fossa located at midpoint of eye and slightly removed from eye (fig. 4A, B). Ocelli small (figs. 1A– C, 2E), separated by about two times diameter of an ocellus, placed at about midpoint of eye in dorsal view, removed from eye by distance slightly greater than diameter of an ocellus (figs. 1A, B, 2E). *Antennae*: Segment 1 (scape) short, only slightly surpassing apex of head (figs. 1A–D, 4A, 6), segments 2 (pedicel), 3, and 4 (flagellum) subequal in length and about three times length of segment 1, segment 1 of slightly greater diameter than segment 2, two times diameter of segments 3 and 4 (figs. 1A–D, 2B, J, 6); no prepedicellite. **Thorax** (figs. 1, 2): Pronotum trapezoidal in dorsal view,

lateral and posterior margins nearly straight (figs. 1A, B); strongly elevated posteriorly, transversely rounded (fig. 2A); collar flat, about as wide as diameter of tibia (figs. 2A, 4A, 6), calli small, ovoid, shining, and devoid of setae, widely separated and placed laterally (fig. 1A, B); posterior lobe well differentiated from callar area (see lateral view, fig. 2A); posterior margin regularly concave (figs. 1A–C, 2C). Scutellum slightly wider than long, nearly flat (figs. 1A, B, 2A, B). Metathoracic scent-gland evaporatory area of limited extent, located anteroventrally on polished metepisternum, attended by a few microtrichia (fig. 4C–E). *Hemelytra* (figs. 1A, B, 2A, K, L, 6A, B): Costal margin of corium weakly sinuous, coriomembranal juncture nearly straight, well defined, and acutely angled anteromedially (fig. 1A–D, 2K, L); venation of corium and clavus obscure, only suggested by thickened costal and scutellar margins; costal fracture obsolete; medial furrow distinct and long (fig. 2A, L); membrane with three straight, longitudinal, "dead" veins, none of them bearing setae (fig. 2K, L, 3C), bases of veins detached from coriomembranal junction; corial process (*processus corial* of Carayon, 1974), or stub (Schuh and Štys, 1991), present sublaterally on membrane at juncture of corium and membrane (fig. 3C); hind wing as in figure 2M; hamus absent. *Corial glands*: Numerous, particularly on posterior half of corium and clavus (figs. 2P, 3D), absent on distalmost part of endocorium; external component in the form of a keyhole with an elongate central mound (figs. 2O, 5A). *Legs*: Femora moderately long, slender, nearly parallel sided, devoid of spines (fig. 2A, B). Foretibia with a cleaning comb on medial surface at apex; no fossula spongiosa. Tarsi elongate (figs. 2A, B, 5C), 3 segmented, segment 1 very short, segments 2 and 3 subequal in length (fig. 5C); fore- and middle tarsi with three strong erect spines on segment 3 (fig. 5C); claws of unequal length, weakly flattened (fig. 5B), major (inner) claw on foreleg very long, much longer than outer claw, shorter on middle leg, and shortest on hind leg (fig. 6C, D, F); parempodia well developed, setiform, of nearly equal length (fig. 5B), of similar structure on all three pairs of legs. **Abdomen** (figs. 1D, E, 5E): Relatively short, broad; sterna entire (fig. 5E); terga (mediotergites) widely separated from dorsal laterotergites (fig. 6A, B); spiracles placed near lateral margin of abdominal sterna on segments 2–8 (fig. 5E). GENITALIA (fig. 5E–G): **Pygophore:** Short, broad, telescoped within abdominal segments 7 and 8, in strong contrast to all genera except *Heissophila and Pavlostysia* (fig. 7A, B); opening of pygophore directed dorsally (figs. 1D, E, 5E, F). **Aedeagus:** Endosoma baglike and inflatable (fig. 1E). **Parameres:** Symmetrical, bulbous at base, apical portion elongate, slender, more or less tubular over most of length, strongly angled at about midpoint, and directed anteromedially (fig. 5G), in contrast to *Heissophila* where apex of paramere directed posterolaterally (Schuh, 2006: figs. 3B, 4C).

Female (fig. 1B): Structure and coloration as in male. Female abdomen with no evidence of sclerotized ovipositor valves (fig. 6A, B), an enlarged vagina (bursa copulatrix) as seen in *Heissophila* (fig. 8B; Schuh, 2006: fig. 4F, G), or copulatory tubes.

Etymology: A combination of Monteith, in honor of Geoff Monteith the collector of many of the known specimens, and the suffix *-phila,* following pattern of generic names previously proposed in the Plokiophilidae. Feminine.

Discussion: *Monteithophila* shares several attributes with *Heissophila*, while at the same time having conditions unique to itself. Shared attributes include the absence of a distinct costal frac-

ture, the structure of the pygophore being similar to that seen in most non-plokiophilid cimiciforms, the exposed angulate parameres lying dorsally on the pygophore, the lack of distinct macrochetae on the frons, vertex, and pronotal collar, the absence of a fossula spongiosa on all tibiae, and the absence of traumatic insemination via copulatory tubes or puncture of the abdominal wall. For this last feature we treat as evidence the saclike inflatable endosoma as seen in figure 1C. Features distinctive to *Monteithophila* are the sinuous costal margin of the corium, the shape of the parameres with their anteromedial orientation rather than posterolateral orientation, and the very long major (inner) claw on the foreleg. Other features of *Monteithophila* include abundant corial glands, incrassate first antennal segment versus stick shaped in *Heissophila*, labial segment 3 longer than 2 as opposed to subequal in *Heissophila*, and all traces of ovipositor lost.

Our examination of the female abdomen macerated in KOH, indicates the absence of the large vagina (bursa copulatrix) seen in *Heissophila* (fig. 8B). This preparation, and a similar preparation for the male, indicate to us that the dorsal abdominal glands are similar to those documented in the adults of *Heissophila* by Schuh (2006) with paired glands present at least on tergum 4 in the male and probably terga 4 and 5 in the female.

Monteithophila queenslandana Schuh, Štys, and Cassis, new species

Figures 1—5

Diagnosis: Recognized by the features listed in the generic description and the largely castaneous coloration. Distinguished from *M. fijiensis,* new species, by the less intensely castaneous coloration and the apparently smaller eyes in that species as well as its occurrence in Fiji.

Description: General coloration castaneous, pronotal collar, costal margin of hemelytron, and antennal segment 1, contrastingly lighter (fig. 1A, B).

Measurements, holotype male: total length 2.41, length head 0.25 , length pronotum 0.35, width head 0.33 , interocular distance 0.21 , width pronotum 0.67.

Measurements, paratype female: total length 2.23, length head 0.20 , length pronotum 0.27, width head 0.34 , interocular distance 0.23 , width pronotum 0.67.

Etymology: Named for it occurrence in Queensland, Australia.

Biotic Association: Some specimens have been collected from the webs of spiders, but no precise identifications of the hosts are available on the labels.

Distribution: Australia: Queensland.

Discussion: See generic discussion under *Monteithophila* and under *M. fijiensis* for comments on size of eyes.

Holotype: **AUSTRALIA: Queensland:** Kirrama, near Smoko Creek, 18.18333°S 145.75°E, 600 m, 09 Mar 2002, C. Jander, 1♂ (AMNH_PBI 00160115) (QM).

Paratypes: **AUSTRALIA: Queensland:** ***N. E. Queensland:*** Peeramon Scrub, 17.31667°S 145.61667°E, 750 m, 09 Dec 1995, G. B. Monteith, 1♂ (AMNH_PBI 00291249) (QM). 3k W of Bones Knob, 17.21667°S 145.4167°E, 1100 m, 10 Dec 1995, Monteith, Cook, Thompson, 1♀ (AMNH_PBI 00291257) (AMNH), 4♂ (AMNH_PBI 00291250-AMNH_PBI 00291253),

1♀ (AMNH_PBI 00291258) (QM). 4.0 km W of Cape Tribulation, site 8, 16.03472°S 145.41917°E, 720 m, 28 Sep 1982, Monteith, Yeates and Thompson, 1♂ (AMNH_PBI 00291247) (AMNH). Danbulla Scientific Reserve, 17.2°S 145.6667°E, 740 m, 02 Nov 1995, G. B. Monteith, 1♀ (AMNH_PBI 00291255) (QM). Kirrama, near Smoko Creek, 18.18333°S 145.75°E, 600 m, 09 Feb 2002, C. Jander, 1♀ (AMNH_PBI 00291246) (AMNH); 09 Mar 2002, C. Jander, 1♀ (AMNH_PBI 00291244), 3♂ (AMNH_PBI 00291242, AMNH_PBI 00291259, AMNH_PBI 00291260) (QM); 17 Mar 2002, C. Jander, 1♂ (AMNH_PBI 00291243), 2♀ (AMNH_PBI 00291245, AMNH_PBI 00160116) (QM). Mt. Misery Summit, via Helenvale, N. Qld., 15.88333°S 145.23333°E, 850 m, 06 Dec 1990, Monteith, Sheridan, Roberts, 1♂ (AMNH_PBI 00291248) (AMNH). U Boulder Ck, 11km NNW of Tully, 17.83333°S 145.9°E, 1000 m, 06 Dec 1989, Monteith, Thompson and Janetzki, 1♀ (AMNH_PBI 00291256) (QM). Wallaman Falls Rd,junction, 18.65°S 145.8667°E, 650 m, 05 Feb 1996, G. Monteith, 1♀ (AMNH_PBI 00291254) (QM). Windsor Tbld, 35km NNW Mt Carbine, 16.25°S 145.1333°E, 1150 m, 15 Apr 1982–18 Apr 1982, Monteith, Yeates, and Cook, 1♂ (AMNH_PBI 00291240), 1♀ (AMNH_PBI 00291241) (QM).

Other Specimens Examined: **AUSTRALIA: Queensland:** Kirrama, near Smoko Creek, 18.18333°S 145.75°E, 600 m, 09 Mar 2002, C. Jander, 1 nymph (AMNH_PBI 00291261) (QM).

Monteithophila fijiensis Schuh, Štys, and Cassis, new species

Diagnosis: Recognized by the features listed in the generic description, the partially castaneous coloration with a pale antennal segment 1 and most of legs, and its occurrence in Fiji. Distinguished from *M. queenslandana* by the more intensely castaneous coloration and relatively larger eyes in that species, as well as its occurrence in northeastern Australia.

Description: Thorax, including pronotum, scutellum, coxae, and antennal segments 2–4 largely castaneous; hemelytron not as heavily castaneous as in *M. queenslandana*. Head, antennal segment 1, and remaining leg segments pale or nearly so (fig. 6). Eyes apparently smaller in *M. fijiensis* than in *M. queenslandana* (see also Discussion below).

Measurements, holotype female: total length 2.33, length head 0.26, length pronotum 0.34, width head 0.32, interocular distance 0.18, width pronotum 0.56.

Etymology: Named for its occurrence in Fiji.

Discussion: Our description of this taxon is based on a single adult female from Fiji; we have also seen two middle-instar nymphs. The female appears to be somewhat teneral, judging from the transparency of the cuticle on the head and abdomen, which may influence our conclusions concerning the size of the eyes, a perception that may be further influenced by observation of the specimen in alcohol as opposed to being pinned and dry. We have chosen to leave the available specimen in alcohol rather than dry mount it, because we believe most necessary observations of morphology would be impaired when dealing with a dry-mounted specimen.

One of us (P. Štys) remembers having examined two additional specimens whose color was metallic dark blue-violet, similar to the various metallic Chrysomelidae or Cydnidae of the genus *Canthophorus* Mulsant and Rey, involving sclerotized parts of the dorsum, head, pronotum, scutellum, corium, clavus, the suggestion of which can be seen in figure 6.

Even though material now available is limited, we describe this taxon to call attention to the occurrence of Plokiophilidae in Fiji and the distribution of *Monteithophila* outside northeastern Australia.

Holotype: **FIJI: Vanua Levu:** Kontiki, 19km E Savusavu, 16.8°S 179.4333°E, 20 m, 19 Jul 1987, Monteith and Cook, 1♀ (AMNH_PBI 00160117) (QM).

Other Specimens Examined: **FIJI: Vanua Levu:** Kontiki, 19km E Savusavu, 16.8°S 179.4333°E, 20 m, 19 Jul 1987, Monteith and Cook, 1 nymph (AMNH_PBI 00291239) (QM).

Heissophila macrotheleae Schuh

Heissophila macrotheleae Schuh, 2006: 637 (n. sp.).

Discussion: Since the publication of the original description of this taxon, additional specimens have become available through the generosity of Peter Schwendinger. Although the specimens from East Kalimantan Province, Borneo, occur some distance from all other known localities for *Heissophila macrotheleae*, we can detect no differences that allow us to treat this material as belonging to a separate species. We have not included unique specimen identifiers for this material.

Additional Specimens Examined: **THAILAND: Chiang Mai Prov.:** Chang Dao Distr.; Doi Chang Dao, limestone cliff between entrances of Chiang Dao Cave and Sua Dao Cave, 19° 23′,33″ N 98° 55′ 56″ E, 450 m, in webs of *Macrothele* sp., 27 Dec 2008, P. Schwendinger, TH-07/21: 10 ♂, 15 ♀ (AMNH, Geneva). **INDONESIA: East Kalimantan Prov.:** Bukit Bangkirai Forest, ca. 30 km N of Balikpapan, 1° 01′ 55″ S 116° 52′ 21″ E, 120 m, primary forest, 8 Oct 2008, P. Schwendinger, IND-08/17: 4 ♂, 1 ♀, 1 nymph (AMNH, Geneva).

Paraplokiophiloides Schuh, Štys, and Cassis, new genus

Type Species: *Paraplokiophiloides schwendingeri*, new species, by present designation.

Diagnosis: Among all Plokiophilidae most similar to *Plokiophiloides* in the possession of long, very slender, 2-segmented tarsi, antennal segment 1 (scape) relatively short and distinctly shorter than segment 2 (pedicel), and in the possession of a tubular pygophore, a feature shared with all members of the Plokiophilinae (see general discussion of classification of Plokiophilidae below). Shares with *Embiophila* spp. the presence of heavy spines on the ventral surface of the fore- and middle femora, but differs from *Embiophila* in having the head with an elongate, parallel-sided neck behind the eyes rather than the weakly exserted head of *Embiophila*, and having very long and slender tarsi rather than being weakly inflated.

Description: *Male*: Small, elongate. SURFACE AND VESTITURE (fig. 7): Vestiture of dorsum and venter comprising short, reclining, simple setae. Antennae with suberect setae of length 2–3 times diameter of segment 2. Head, in addition to other erect setae, with two pairs of conspicuously long, erect, curving setae, one pair situated at level of posterior margin of clypeus, the other pair between ocellus and eye at posterior margin of eye (fig. 7A); pronotal collar anterolaterally with a long, posteriorly directed macrocheta (fig. 7A, B) as recorded by Carayon (1974) for other Plokiophilinae; abdominal segment 8 with ~6 elon-

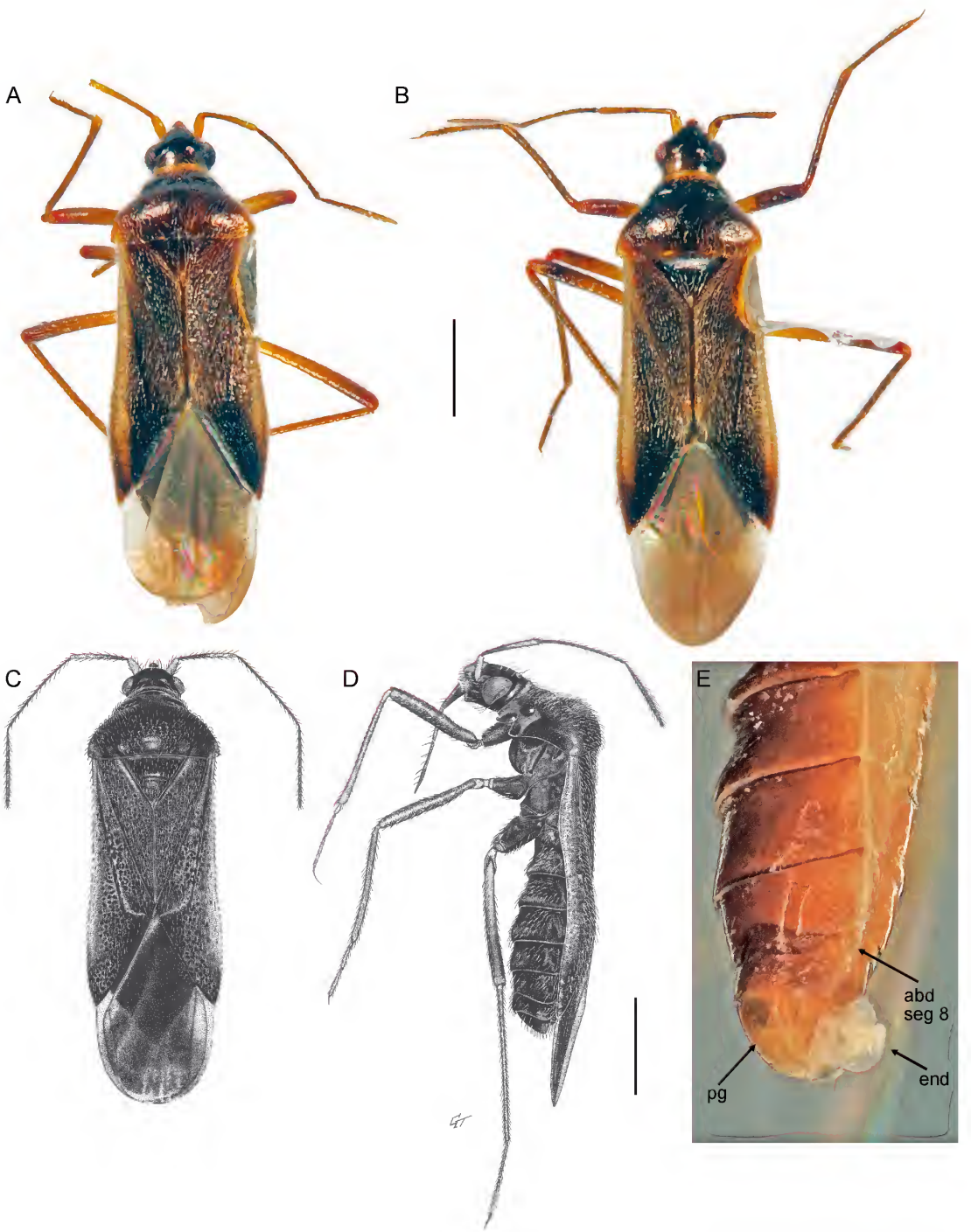

FIG. 1. *Monteithophila queenslandana*. **A.** Male (AMNH_PBI 00160115). **B.** Female (AMNH_PBI 00160116). **C.** Male, illustration of dorsal habitus. **D.** Male, illustration in lateral view. **E.** Left lateral view of male abdomen showing pygophore and inflated endosoma. Abbreviations: **abd seg 8,** abdominal segment 8; **end,** endosoma; **pg,** pygophore.

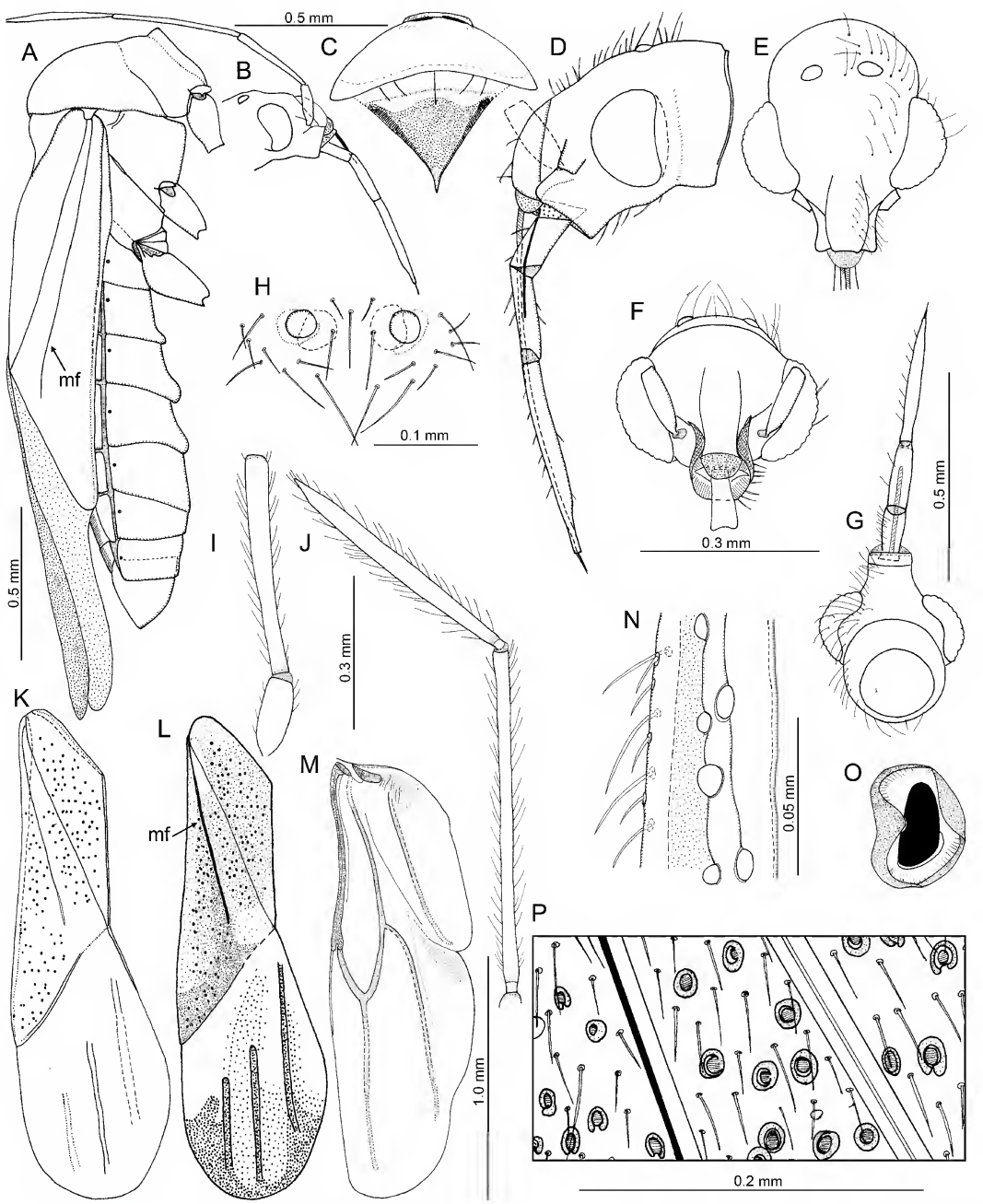

FIG. 2. Morphological details of *Monteithophila queenslandana*. **A.** Right lateral view of male body, head removed. **B.** Right lateral view of head, including antenna. **C.** Pronotum and scutellum, dorsal view. **D.** Left lateral view of head, including labium. **E.** Dorsofrontal view of head, including ocelli and clypeus. **F.** Frontal view of head, including antennal segment 1. **G.** Posterior view of head (removed from body), including rostrum. **H.** Detail of ocelli, including surrounding setae. **I.** Scape and pedicel. **J.** Flagellum. **K.** Left forewing. **L.** Left forewing, indicating medial furrow. **M.** Left hind wing. **N.** Costal margin of forewing, showing campaniform sensilla. **O.** Detail of corial gland. **P.** Corial glands on forewing. Abbreviation: **mf,** medial furrow.

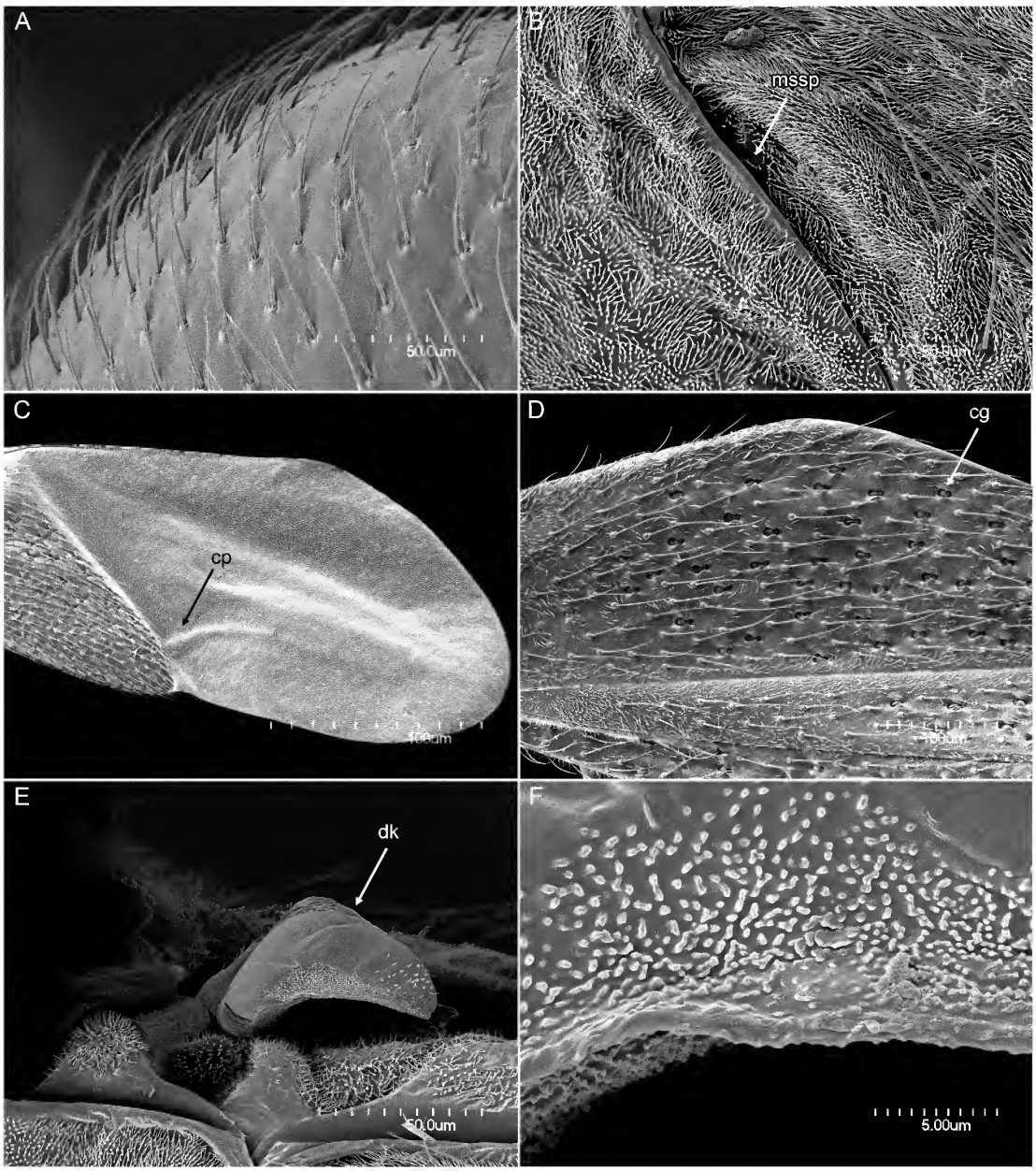

FIG. 3. Scanning electron micrographs of *Monteithophila queenslandana*. **A.** Pronotum, showing reclining simple setae. **B.** Mesothoracic spiracle opening (mssp). **C.** Left hemelytron showing "cuneus," membrane, and corial process (cp). **D.** Corium and clavus of left wing showing setation and corial glands (cg). **E.** Forewing-locking mechanism on mesothorax, indicating druckknopf. **F.** Detail of surface structure of druckknopf. Abbreviations: **cg,** corial gland; **cp,** corial process; **dk,** druckknopf; **mssp,** mesothoracic spiracle.

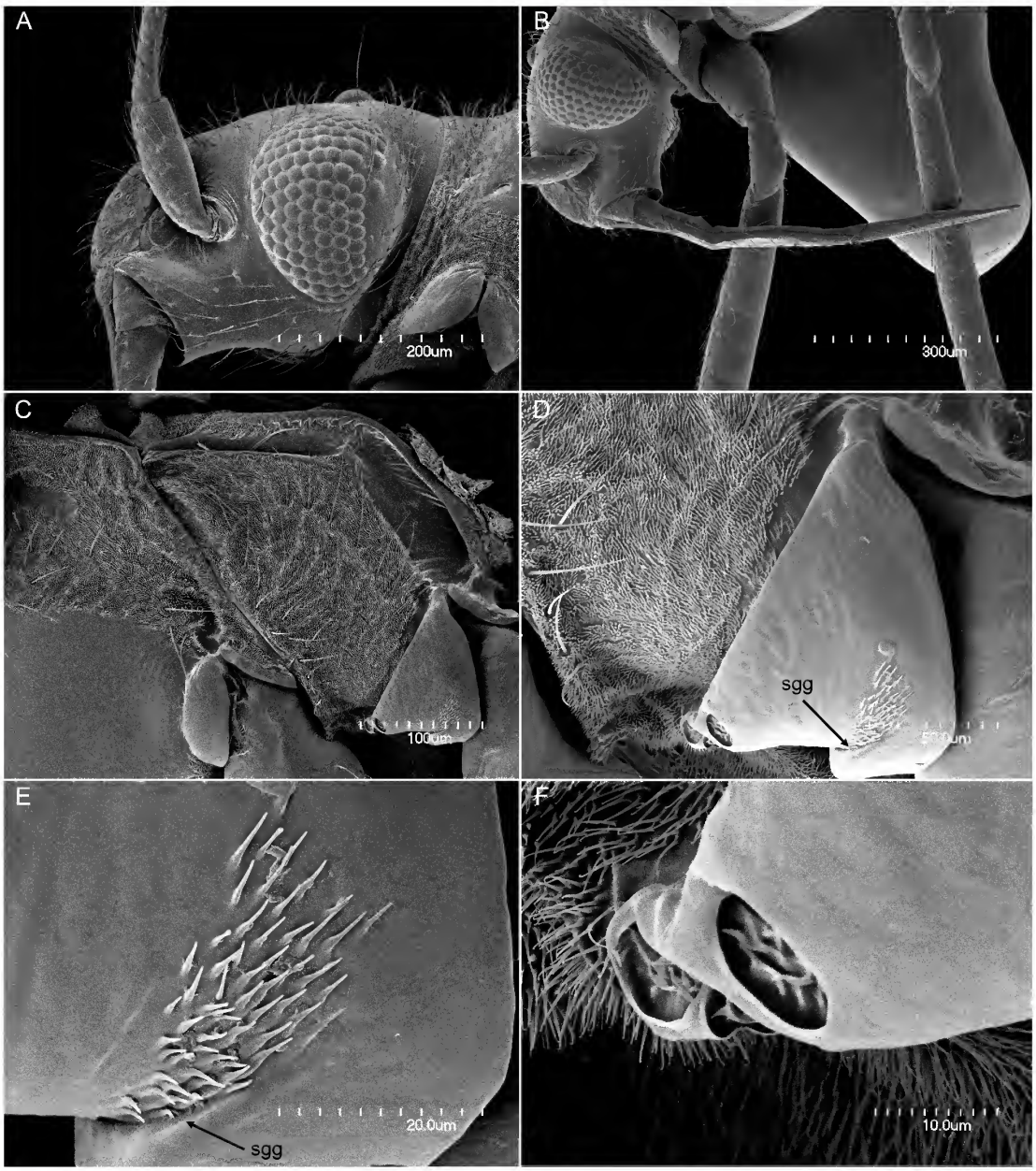

FIG. 4. Scanning electron micrographs of *Monteithophila queenslandana*. **A.** Left lateral view of head, pronotal collar, and foreacetabulum. **B.** Left lateral view of head and rostrum. **C.** Left lateral view of meso- and metathorax. **D.** Left lateral view of metathorax, including scent-gland groove with spicula on peritremal area. **E.** Detail of scent-gland groove. **F.** Detail of ventral portion of metapleuron. Abbreviations: **sgg,** scent gland groove.

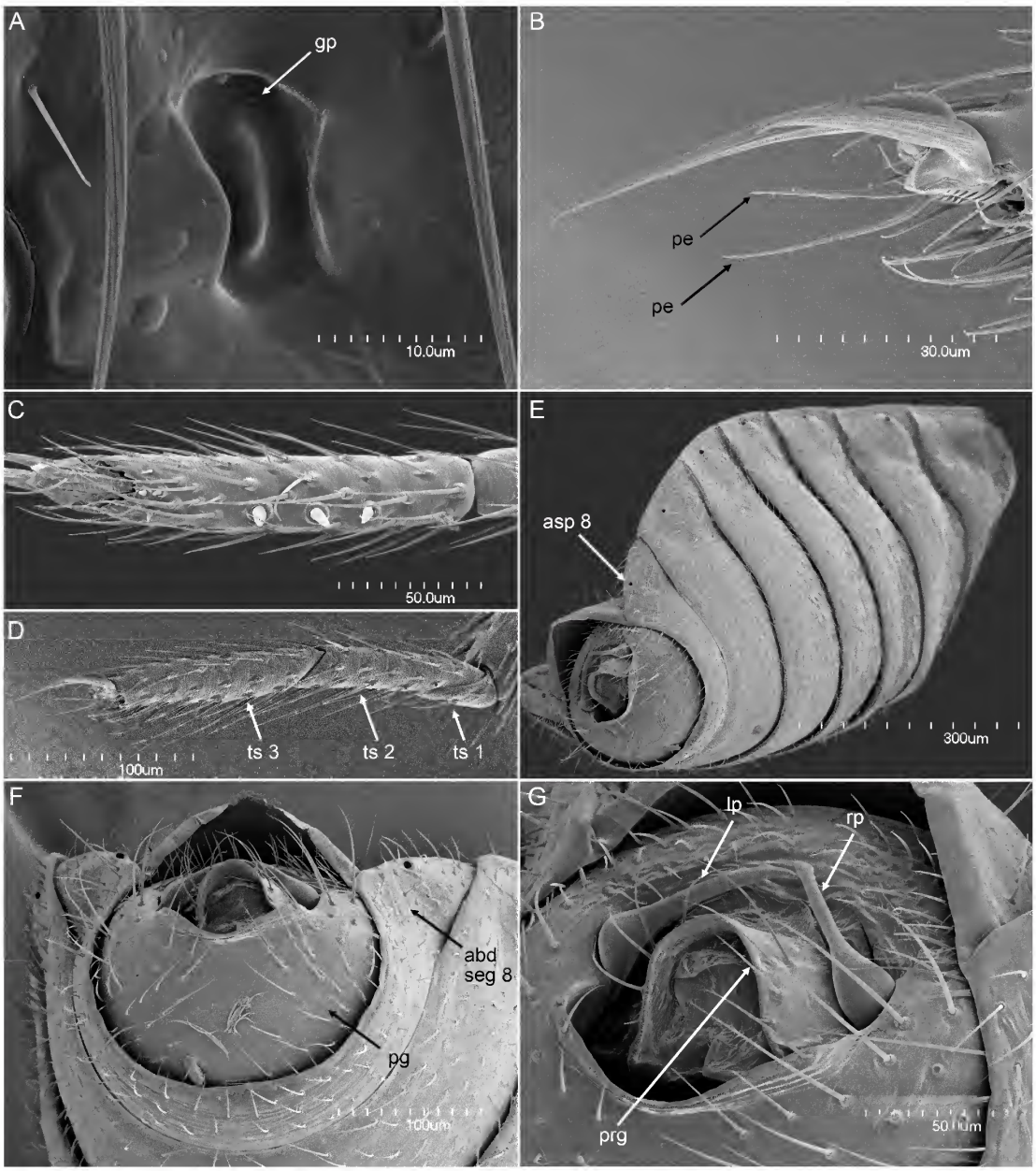

FIG. 5. Scanning electron micrographs of *Monteithophila queenslandana.* **A.** Detail of corial gland. **B.** Claws of middle leg, showing strong asymmetry, and parempodia. **C.** Ventral surface of tarsal segment 3 of foreleg, showing heavy peglike setae. **D.** Tarsus and pretarsus of middle leg, showing 3-segmented condition. **E.** Posteroventral view of male abdomen, including pygophore, showing spiracles on fused laterotergites + mediosternites. **F.** Posterior view of pygophore. **G.** Detail of proctiger and parameres, in situ. Abbreviations: **abd seg 8,** abdominal segment 8; **asp 8,** abdominal spiracle 8; **gp,** gland pore; **lp,** left paramere; **pe,** parempodia; **pg,** pygophore; **prg,** proctiger; **rp,** right paramere; **ts 1,** tarsal segment 1; **ts 2,** tarsal segment 2, **ts 3,** tarsal segment 3.

FIG. 6. *Monteithophila fijiensis*, holotype female (AMNH_PBI 00160117). **A.** Right lateral view. **B.** Left lateral view. **C.** Left lateral view of head, fore- and middle legs. **D.** Right lateral view of head, fore- and middle legs. **E.** Detail of forelegs. **F.** Detail of hind tarsus. Abbreviations: **ftc,** foretarsal claw; **mtc,** mesotarsal claw; **ts 1,** tarsal segment 1; **ts 2,** tarsal segment 2.

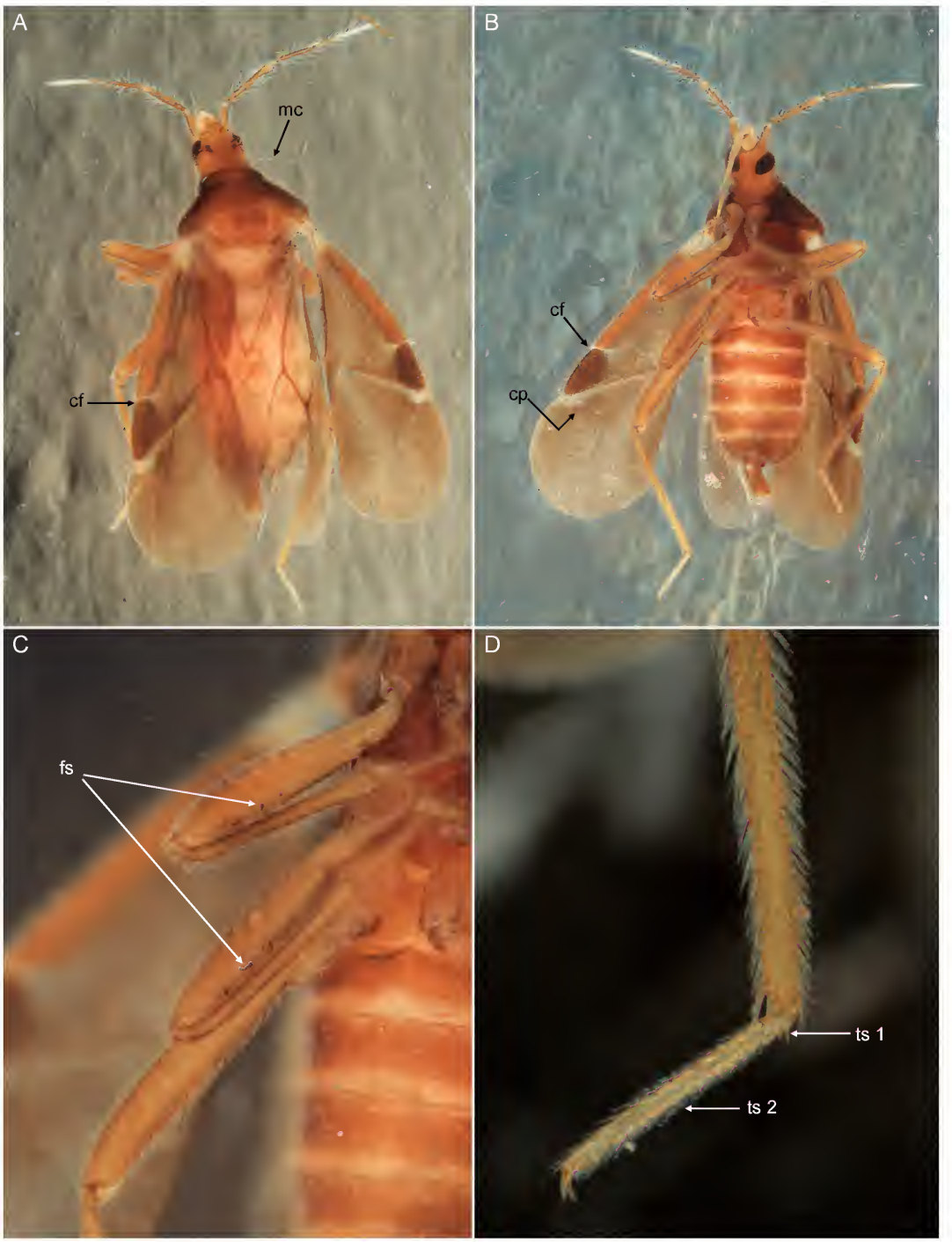

FIG. 7. *Paraplokiophiloides schwendingeri*, holotype male (AMNH_PBI 00413046). **A.** Dorsal view. **B.** Ventral view. **C.** Lateral ventral surface of fore-, middle, and hind femora, showing peglike spines on fore and middle femora. **D.** Detail of 2-segmented hind tarsus. Abbreviations: **cf,** costal fracture; **cp,** corial process; **fs,** femoral spines; **mc,** macrocheta; **ts 1,** tarsal segment 1; **ts 2,** tarsal segment 2.

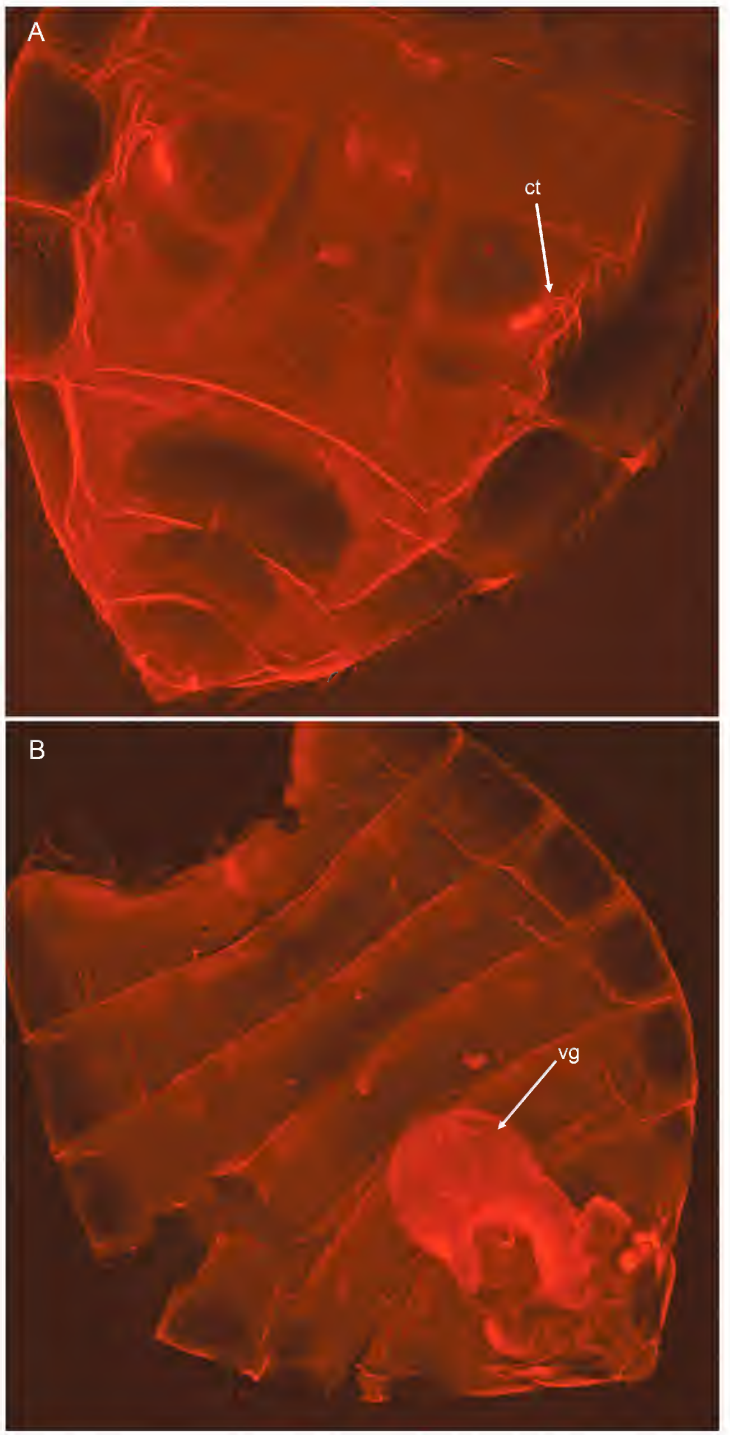

FIG. 8. Laser confocal microscopic images. **A.** *Lipokophila eberhardi*, female abdomen showing copulatory tubes. **B.** *Heissophila macrotheleae*, female abdomen, showing large asymmetrical "vagina" and absence of copulatory tubes. Abbreviations: **ct,** copulatory tube; **vg,** vagina (bursa copulatrix).

gate setae laterally (fig. 7B), but without a distinct, very long macrocheta. STRUCTURE: **Head** (fig. 7A, B): Elongate anteroposteriorly, cylindrical, behind eye in the form of a neck, projecting beyond anterior margin of eye by about the length of eye; buccal cavity more or less round, directed anteroventrally, greatly removed from posterior margin of head by gula of length about 2.5 times diameter of eye (fig. 7B); mandibular and maxillary plates small; buccula very narrow (fig. 7B). Labium, slender, tapering to acute apex, reaching to about midpoint of mesosternum, segment 1 short and broad, well developed (fig. 7B), ratio of length of segments 1:3:4:7. Eyes relatively small in dorsal view, removed from anterior margin of pronotum by about longitudinal diameter of eye; eye in lateral view occupying entire height of head, elongate oval in outline, anterior and posterior margins nearly straight; antennal fossa located just below midpoint of eye and slightly removed from eye (fig. 7A, B). Ocelli large (fig. 7A), widely separated, placed at level of posterior margin of eye, barely removed from eye (fig. 7A). *Antennae:* Segment 1 relatively short, just surpassing apex of clypeus (fig. 7A), segments 2, 3, and 4 subequal in length and distinctly longer than segment 1, slender, segment 2 of slightly smaller diameter than segment 1, segments 3 and 4 subequal in diameter, of slightly smaller diameter than segment 2; prepedicellite present as a narrow sclerotized band at base of segment 2. **Thorax** (fig. 7): Pronotum campanulate, collar distinct, flattened; anterior lobe narrow but distinct, posterior lobe strongly elevated, poster margin strongly excavated across scutellum and convexly rounded laterally (fig. 7A); scutellum slightly wider than long (fig. 7A). Metathoracic scent-gland groove extending just onto metepisternum, evaporatory area of limited extent, apparently in the form of a few reclining spicules (this structure noted as not discernible in *Lipokophila* by Štys [1967], but see figure 4D, E for *Monteithophila queenslanda* and Schuh [2006: fig. 3D] for *Heissophila macrotheleae*). *Hemelytra* (fig. 7A, B): Costal margin of corium weakly convex; costal fracture located about three-fourths distance from base to apex of corium, demarcating cuneus but without deep incisure, just interrupting strongly sclerotized part of exocorium, not reaching medial furrow (fig. 7A, B), medial furrow pronounced fig. 7A, B); coriomembranal juncture nearly straight, well defined, and angled anteromedially (fig. 7A, B membrane without longitudinal veins (fig. 7A, B); corial process visible ventrally on membrane as an elongate, sublateral, veinlike structure (fig. 7B). *Corial glands*: Present on exocorium and cuneus, reservoir visible with transmitted light under dissecting microscope; exact number and distribution not documented. *Legs*: Relatively short. Femora of moderate length, weakly robust, fore- and middle femora with a few short, heavy spines on distoventral surface, hind femur mutic. Fore- and middle tibiae with a cleaning comb on lateral surface at apex and with a fossula spongiosa; hind tibia without fossula spongiosa; tarsi long, very slender, 2-segmented, segment 1 very short, segment 2 greatly elongate (fig. 7D). Claws elongate and of similar length on all legs, inner claw longer than exterior; parempodia apparently well developed, setiform. **Abdomen** (fig. 7B): Elongate; sterna entire, terga (mediotergites) widely separated from dorsal laterotergites by a broad membranous area; spiracles placed on sternum near lateral margin of abdominal segments 2–8. GENITALIA (figs. 7A, B): **Pygophore:** Tubular, erect (fig. 7A, B), similar in form to other taxa placed in the Plokiophilinae. **Aedeagus:** Endo-

soma enclosed within pygophore. **Parameres:** Symmetrical or nearly so, almost completely enclosed within pygophore.

Female: Similar to male except for terminal abdominal segments. Abdominal sternum 7 truncate posteromedially, weakly sinuous laterally.

Etymology: Named for its similarity in appearance to *Plokiophiloides* Carayon.

Biotic Association: Known to occur only in the webs of *Macrothele* Ausserer (Araneae: Mygalomorphae: Hexathelidae).

Distribution: Thailand: Chang Rai Province.

Discussion: Although this taxon shares many morphological similarities with *Plokiophiloides* Carayon, including the relatively short antennal segment 1, the longer antennal segment 2, the 2-segmented tarsi, the paired macrochetae on the pronotal collar and head, and the erect, tubular pygophore, treating these attributes as potential synapomorphies is contradicted by the presence of several heavy spines on the fore- and middle femora as seen elsewhere only in *Embiophila* China. Carayon (1974) treated the femoral spines as diagnostic for the Embiophilinae, along with their being inhabitants of embiid webs (see also comments under on classification under Discussion below).

Paraplokiophiloides schwendingeri Schuh, Štys, and Cassis, new species

Diagnosis: See generic diagnosis.

Description: COLORATION (fig. 1A, B): Dark brown, antennal segment 1, pronotal collar, and costal margin of corium pale. GENITALIA: As indicated in generic description; not dissected.

Measurements, male: total length 2.50, length head 0.35, length pronotum 0.31, width head 0.30, interocular distance 0.18, width pronotum 0.72.

Measurements, female: total length 2.50, length head 0.25, length pronotum 0.30, width head 0.30 interocular distance 0.18, width pronotum 0.73.

Etymology: Named in honor of Peter Schwendinger, Geneva, who collected the only known specimens.

Biology: Known from the web of *Macrothele* sp. (Araneae: Megalomorphae: Hexathelidae).

Distribution: Thailand: Chang Rai Province.

Discussion: We have seen only two specimens of *Paraplokiophiloides*, collected from the web of *Macrothele* sp. On the other hand, we have examined many specimens of *Heissophila macrothelae* from the webs of the same host, suggesting to us that *Paraplokiophiloides* may prefers the webs of another spider or that they simply have smaller populations on a given web than *Heissophila*. We encourage those doing fieldwork on spiders in tropical Asia to keep their eyes open for these tiny commensals.

Holotype: **THAILAND: Chang Rai Prov.:** Mae Sai District: Doi Tung, 20.31666°N 99.81666°E, 1300 m, 13 Oct 1994, P. J. Schwendinger, 1♂ (AMNH_PBI 00413046) (AMNH).

Paratypes: **THAILAND: Chang Rai Prov.:** Mae Sai District: Doi Tung, 20.31666°N 99.81666°E, 1300 m, 13 Oct 1994, P. J. Schwendinger, 1♀ (AMNH_PBI 00413047) (AMNH).

DISCUSSION

The classification of Plokiophilidae as codified by Carayon (1961, 1974) included two subfamilies, Plokiophilinae and Embiophilinae. The chief characteristics distinguishing them were the mutic forefemora and the occupation of spider webs in the former group and the armed forefemora and the occupation of webs of Embiidina in the latter. The structure of the male and female genitalia in both groups was documented by Carayon (1974) to be substantially similar, the males possessing an acus as the terminal portion of the aedeagus, the parameres being elongate, more or less parallel sided, nearly straight and largely enclosed within the pygophore, and the female either possessing copulatory tubes anteriorly or medially in the abdomen or with evidence of copulatory scars.

Schuh (2006) showed that the male genitalia of *Heissophila* from Thailand were unlike those seen in any previously described members of the Plokiophilidae and that the taxon could not be accommodated in either the Plokiophilinae or Embiophilinae as defined by Carayon (1961, 1974). He speculated that the symmetrical and apparently inflatable phallus, in combination with the symmetrical grasping-style parameres would seem to render these insects incapable of traumatic insemination. Our examination of *Monteithophila* indicates many similarities in morphology with *Heissophila*, including the apparent absence of structures associated with traumatic insemination as seen in the members of Plokiophilidae studied by Carayon (1961, 1974).

Schuh (2006) further showed that *Hessophila* lived in the webs of mygalomorph spiders in the genus *Macrothele* (Hexathelidae), based on the collecting observations of Peter Schwendinger. *Plokiophila cubana* (China and Myers) from Cuba, was previously the only plokiophilid known to live in mygalomorph webs, in that case in webs of the family Dipluridae (China and Myers, 1929).

Because Schuh (2006) did not establish a revised classification that satisfactorily accommodates *Heissophila*, because we now have knowledge of the morphologically similar taxon *Monteithophila* from Australia, because we now have definitive evidence for the presence of Plokiophilidae in the fossil record (Popov, 2008), and because we have documentation for *Paraplokiophiloides*, which also does not fit comfortably in the classification of Carayon (1961, 1974), we offer additional observations and argumentation in the presentation of a revised classification for the Plokiophilidae.

Female copulatory and genitalic morphology: We have used confocal laser microscopy to further investigate the nature of genitalic morphology in the Plokiophilidae. Our observations indicate that *Hessophila* (fig. 8B) lacks copulatory tubes, as was surmised by Schuh (2006), but for which we now have definitive observations. As noted above, our observations corroborate similar morphology for *Monteithophila*. In order to place these observations in a comparative context, we have also produced laser confocal observations for *Lipokophila eberhardi* Schuh, a plokiophiline, which has well-developed copulatory tubes associated with abdominal segment 5 (fig. 8A). We stress that the absence of copulatory tubes in females is not limited to the genera *Heissophila* and *Monteithophila*, the only plokiophilid genera in which the traumatic insemination is absent. As evidenced by the presence of dorsoabdominal copulatory scars ("cicatrices" of Carayon, 1974) on the desclerotized or little sclerotized mediotergites or intersegmental membranes—usually on abdominal segments 4 and 5—traumatic insemination occurs in spe-

cies of the *Plokiophiloides asolen* group and in mostly undescribed Old World species of *Embiophila (Acladina)* even when copulatory tubes are absent (Carayon, 1974, Štys, 1991). On the other hand, copulatory tubes are present in species of the *Plokiophiloides biforis* group (Štys 1991; Afrotropical and Madagascan) and in New World in species of *Embiophila (Embiophila)*, with two described species (Carayon, 1974; Carpintero and Dellapé, 2005).

The confocal image of the abdomen of *Lipokophila* (fig. 8) indicates that there are no sclerotized ectodermal structures in the abdomen. On the other hand, the image of *Heissophila* shows a well-developed, asymmetrical "vagina" (bursa copulatrix) (but also see illustrations in Schuh, 2006, indicating a symmetrical structure) suggesting additional corroboration for the existence of insemination through the insertion of the phallus into this structure in the female.

Male genitalic morphology: The male genitalia of Plokiophilidae sensu stricto were well documented by Carayon (e.g., 1974). Schuh (2006) provided documentation showing the profound differences between the male genitalia of *Heissophila* and all other described taxa of Plokiophilidae. What he was not able to show by direct observation was the manner in which the phallus of *Heissophila* might function. Nonetheless, one alcohol-preserved specimen of *Monteithophila* offers potential evidence for phallic function in these two genera, with the inflation of what we believe is the endosoma, as shown in figure 1C. After examination of more than 50 alcohol-preserved male specimens of *Heissophila* we have not found any males with a distended phallus. We nonetheless predict that in light of the many other similarities shared by these two taxa that the method of phallic function in both must be similar.

Revised classification of the Plokiophilidae: Schuh (2006) chose to leave the issue of higher classification of the Plokiophilidae unaddressed until a future time. Although we believe additional discoveries of plokiophilid diversity may still come to light, the description of *Monteithophila* and *Paraplokiophiloides* in this paper and *Pavlostysia* by Popov (2008) offers additional evidence on which to formalize a revised classification of the group.

Whereas Carayon (1961, 1974) thought traumatic insemination was a defining character for the Plokiophilidae, our confocal microscopic studies corroborate Schuh's (2006) conclusion that this attribute is not present in *Heissophilia,* and by extension, in *Montheithophila.* In accordance with the arguments of Schuh (2006), we nonetheless concur that on the basis of other characters, including corial glands, claw structure, and head structure, that the Plokiophilidae—including *Heissophila* and *Monteithophila*—form a monophyletic group.

The work of Carayon (1974), especially as interpreted by Ford (1976) and presented by Schuh (1986) and Schuh and Štys (1991), suggested that traumatic insemination was a diagnostic feature for a monophyletic group including all members of Cimicoidea other than Lasiochilidae. More recent phylogenetic studies (Schuh et al., 2009), and the discovery of new taxa such as *Curalium* Schuh et al. (2008) and *Heissophila*, have drawn this conclusion into question, suggesting that either traumatic insemination has evolved several times within the cimicoid lineage, or that it has been lost in *Heissophila* + *Monteithophila*, and *Curalium*.

In the following classification we postulate diagnostic characters for the various higher taxa, this in the absence of a rigorous phylogenetic analysis. It is our view that this scheme offers a stronger argument for characters that define the groups, with the admission that the apparently homoloplastic nature of character distributions in the Plokiophilidae, and the Cimi-

coidea more broadly, militates for additional testing of our hypotheses of group monophyly:

Plokiophilidae China, 1953

Diagnosis: Head more or less cylindrical; hemelytron, and sometimes other areas of body, with corial glands; claws of unequal length; living in webs and possibly more rarely free-living (see addendum).

Heissophilinae Schuh, Štys, and Cassis, **new subfamily**

Diagnosis: Pygophore broadened basally and somewhat flattened dorsoventrally, parameres symmetrical, with a basal shaft and a right-angled apical portion; phallus inflatable (based on *Monteithophila*) and lacking a sclerotized acus; female lacking copulatory tubes; head and pronotal collar lacking macrochetae; tarsi 3-segmented; fossula spongiosa absent; no traumatic insemination as deduced from morphological observations; costa entire, no cuneus present in Recent fauna, but costal fracture present in *Pavlostysia*.

Heissophila Schuh, 2006

Monteithophila Schuh, Štys, and Cassis

Pavlostysia Popov, 2008, Baltic amber fossil

Plokiophilinae China, **sensu novo**

Diagnosis: Pygophore tubular, erect, parameres elongate, slender, nearly straight, largely enclosed within pygophore; apical portion of phallus not inflatable, in the form of an acus; female with or without copulatory tubes; head and pronotal collar with multiple paired macrochetae; tarsi 2 or 3-segmented; fossula spongiosa present on fore and middle tibiae; with traumatic insemination as deduced from direct observation and morphology; costal fracture and distinct cuneus always present.

Lipokophilini, Schuh, Štys, and Cassis, **new tribe**

Diagnosis: Tarsi 3-segmented, antennal segment 1 very long, length greater than width of head including eyes, and antennal segment 2 longer than seen in all other taxa; copulatory tubes located in abdominal segment 5.

Lipokophila Štys, 1967

Plokiophilini China, **revised status**

Diagnosis: Tarsi 2-segmented, antennal segment 1 short, not or barely exceeding apex of head and equal to or less than interoccular distance, antennal segment 2 less than two times length of segment 1; copulatory tubes located in abdominal segment 2 or absent.

Plokiophilina, **revised status**

Diagnosis: All femora mutic; found in the webs of spiders or free-living (see discussion below)

Plokiophila China and Myers, 1929

Plokiophiloides Carayon, 1974

Embiophilina Carayon, 1961, **revised status**

Diagnosis: Fore- and middle femora with heavy spines on distoventral surface; found in the webs of embiids or more rarely spiders.

Embiophila China, 1953

Paraplokiophiloides Schuh, Štys, and Cassis

We place the Baltic amber *Pavlostysia*, the only fossil taxon that can be placed in the Plokiophilidae with confidence, in the Heissophilinae on the basis of its short pygophore that is broadly connected to the abdomen, opens dorsally, and has the parameres lying dorsally; these attributes are not visible in the photograph of the holotype and were not part of Popov's (2008) illustration, but they were clearly stated in his description. This placement of this taxon is further supported by the 3-segmented tarsi, short antennae, and the lack of a macrochetae laterally on the pronotal collar. *Pavlostysia* lacks membrane venation seen in other members of the Heissophilinae, but has mutic forefemora. It has the longest known labium in the family, which reaches to abdominal segment 3. Popov (2008) commented that the costal fracture in *Pavlostysia* is distinct and long and that the cuneus is weakly distinct. This condition is unlike that seen in other members of the Heissophilinae, where there is no evidence of a costal fracture, as opposed to members of the Plokiophilinae where there is always a distinct costal fracture demarcating a cuneus (fig. 7A, B).

We observe that there might be reason to treat the subgenera of *Embiophila* as recognized by Carayon (1974) and the species groups of *Plokiophiloides* as distinct genera because of the presence or absence of copulatory tubes in the female. We refrain from doing so at the present time, however, believing that this action should be based on a more extensive descriptive record of the species belonging to these groups.

Key to males for the higher taxa and genera of Plokiophilidae

1. Tarsi 3-segmented; shape of pygophore variable; cuneus present or absent 2
– Tarsi 2-segmented; pygophore always tubular; hemelytron with a distinct cuneus (Plokiophilinae: Plokiophilini) 5
2. Pygophore at least weakly flattened dorsoventrally, broader at base than at apex, parameres with a strong angle, lying on dorsal surface of pygophore in repose; macrochetae absent from vertex and frons and from anterolateral angles of pronotum; antennal segment 1 short, length less than interoccular distance; fossula spongiosa absent on all legs; cuneus present or absent (Heissophilinae) 3
– Pygophore tubular, of similar diameter over entire length, parameres nearly straight, needlelike, and surrounded by pygophore except at apex; macrochetae present on head and on anterolateral angle of thorax; antennal segment 1 very long, equal to or greater than width of head including eyes; fossula spongiosa present on fore- and middle tibiae; cuneus present (Plokiophilinae: Lipokophilini) . . . . . *Lipokophila* Štys
3. Head tubular in dorsal view, necklike behind eyes; membrane of hemelytron without evidence of veins; cuneus present . . . . . *Pavlostysia* Popov
– Head not distinctly tubular in form, without neck behind eyes, posterior margin of eye very close to pronotal collar; membrane of hemelytron with three or four free veins; cuneus absent 4
4. Apex of paramere directed anteromedially; membrane of hemelytron with three weakly developed free veins . . . . . *Montheithophila* Schuh, Štys, and Cassis

– Apex of paramere directed posterolaterally; membrane of hemelytron with four conspicuous free veins ..... *Heissophila* Schuh
5. Fore- and middle femora mutic (Plokiophilina) 6
– Fore- and middle femora with heavy spines on distoventral surface (Embiophilina) 7
6. Posterior margin of pronotum straight across between humeral angles; posterior margin of abdominal tergum 8 with a dorsally directed hornlike process on either side of pygophore ..... *Plokiophila* China
– Posterior margin of pronotum excavated across broadly exposed mesoscutum; posterior margin of abdominal tergite 8 without hornlike ornamentation.. *Plokiophiloides* Carayon
7. Head without an elongate neck behind eyes; legs relatively short and stout; tarsi relatively short ..... *Embiophila* China
– Head with an elongate neck behind yes; legs relatively long and slender; tarsal segment 2 very long and slender ..... *Paraplokiophiloides* Schuh, Štys, and Cassis

ACKNOWLEDGMENTS

We thank Geoff Monteith, Queensland Museum, Brisbane, for the loan of specimens of *Monteithophila* studied during the preparation of this paper and for his dedication in collecting this novel taxon. We also thank Peter Schwendinger, Natural History Museum, Geneva, for making available specimens of *Heissophila macrothelae* and *Paraplokiophiloides* from Thailand and acknowledge the value of his dedication to capturing these tiny web-inhabiting commensals as part of his arachnological studies. We thank Steve Thurston (AMNH) for preparing the digital habitus images and for assembly of all illustrations, Morgan Hill and Henry Towbin of the Microscopy and Imaging Facility (AMNH) for assistance in preparing the scanning electron micrographs, Ruth Salas for preparing the specimen measurements, and Lily Berniker and Norman Platnick for use of their time and equipment in preparing the images of *Monteithophila fijiensis* and *Plokiophiloides schwendingeri*. P.Š. thanks the Czech Science Foundation for financial support from grant P505/11/1455. We also thank the two reviewers of the manuscript for helping to clarify inconsistencies and improve the overall nature of our presentation.

REFERENCES

Borkent, A., and G.R. Spinelli. 2007. Neotropical Ceratopogonidae (Diptera: Insecta). *In* J. Adis, J.R. Arias, G. Rueda-Delgado, and K.M. Wantzen (editors), Aquatic biodiversity in Latin America, vol. 4. Sofia, Bulgaria: Pensoft Publishers. 198 pp.

Carayon, J. 1961. La viviparité chez les Hétéroptères. Verhanglungen: XI Internationaler Kongress für Entomologie, Wien 1: 711–714 (1960).

Carayon, J. 1974. Etude sur les hémiptères Plokiophilidae. Annals Société Entomologique de France (N.S.) 10 (3): 499–525.

Carpintero D.L., and P.M. Dellapé. 2005. A new species and first record of *Embiophila* (Heteroptera: Plokiophilidae) from Nicaragua. Studies of Neotropical Fauna and Environment 40: 65-68.

China, W.E. 1953. A new subfamily of Microphysidae (Hemiptera-Heteroptera). Annals and Magazine of Natural History (12) 6: 97–125.

China, W.E., and J.G. Myers. 1929. A reconsideration of the classification of the cimicoid families (Heteroptera), with the description of two new spider-web bugs. Annals and Magazine of Natural History (10) 3: 97–125.

Eberhard, W.G., N.I. Platnick, and R.T. Schuh. 1993. Natural history and systematics of arthropod symbionts (Araneae; Hemiptera; Diptera) inhabiting the webs of the spider *Tengella radiata* (Araneae, Tengellidae). American Museum Novitates 3065: 1–17.

Ford, L.J. 1976. The phylogeny and biogeography of the Cimicoidea (Insecta: Hemiptera). Master's thesis, University of Connecticut, Storrs, 138 pp.

Jung, S., and S. Lee. 2012. Correlated evolution and Bayesian divergence time estimates of the Cimicoidea (Heteroptera: Cimicomorpha) reveal the evolutionary history. Systematic Entomology 37: 22–31.

Jung, S., H. Kim, K. Yamada, and S. Lee. 2010. Molecular phylogeny and evolutionary habitat transitions in flower bugs (Heteroptera: Anthocoridae). Molecular Phylogenetics and Evolution 57: 1173–1183.

Popov, Y.A. 2008. *Pavlostysia wunderlichi* gen. nov. and sp. nov., the first fossil spider-web bug (Hemiptera: Heteroptera: Cimicomorpha: Plokiophilidae) from the Baltic Eocene Amber. Acta Entomologica Musei Nationalis Pragae 48: 497–502.

Schuh, R.T. 1986. The influence of cladistics on the classification of the Heteroptera. Annual Review of Entomology 31:67–93.

Schuh, R.T. 2006. *Heissophila macrotheleae*, a new genus and new species of Plokiophilidae from Thailand (Hemiptera, Heteroptera), with comments on the family diagnosis. Denisia 19: 637–645.

Schuh, R.T. and J.A. Slater. 1995. True bugs of the world (Hemiptera: Heteroptera), classification and natural history. Ithaca, NY: Cornell University Press, 336 pp.

Schuh, R.T. and P. Štys. 1991. Phylogenetic analysis of cimicomorphan family relationships. Journal of the New York Entomological Society 99: 298–350.

Schuh, R.T., C. Weirauch, T.J. Henry, and S.E. Halbert. 2008. A new family of Heteroptera from the Eastern United States (Insecta). Annals of the Entomological Society of America, 101: 20–29.

Schuh, R.T., C. Weirauch, and W.C. Wheeler. 2009. Phylogenetic analysis of family-group relationships in the Cimicomorpha (Hemiptera). Systematic Entomology 34: 15–48.

Štys, P. 1967. *Lipokophila chinai* gen. n., sp. n. – a new genus of Plokiophilidae (Heteropera) from Brazil. Acta Entomologica Bohemoslovaca 64: 248–258.

Štys P. 1991. The first species of Plokiophilidae from Madagascar (Heteroptera, Cimicomorpha). Acta Entomologica Bohemoslovaca 88: 425–430.

ADDENDUM

Petr Baňař has recently collected the Plokiophilidae at several rainforest localities on Madagascar. One of the commonest *Plokiophiloides* species (*biforis* group, with a unique type of dorsal basi-abdominal copulatory tubes) is undescribed, and was found to be free-living and collected in numbers by sieving the litter in which no web-forming species of spiders or embiopterans were present. The results are being prepared for publication by P. Štys and P. Baňař.